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Four hybrids of Viola pedatifida

EZRA BRAINERD

(WITH PLATES 15–17)

The hybrids between *Viola pedatifida* and allied species are in several respects the most interesting among the 75 or 80 that have appeared in the genus as represented in North America. At least two of the four are remarkably hardy, almost immune from attacks of fungus, and comparatively fertile; they are therefore well suited for experimental cultures. The marked contrast in leaf outline displayed in the parents of the several crosses affords a fine opportunity for studying in detail the many diverse forms of leaf that emerge in the offspring of the hybrid. The other opposed parental characters, relating to pubescence, color of capsule, color of seed, length of peduncle, and villosity of spur petal, also lead to results well worthy of careful study.

One of these hybrid plants I have had in hand for eight seasons and have raised from it over 450 offspring, extending through four generations. It was discovered at Yorkville, Ill., May 1905, by Miss Mary O. Pollard, a former pupil, and may be briefly described as follows:

1. **Viola papilionacea** × **pedatifida** hyb. nov.

Rootstock stout, at length extensively branching horizontally; leaves broadly deltoid-ovate in outline, cleft into 7–11 linear or oblong lobes, the middle lobe much the widest, glabrous, though the margins are often scabro-ciliolate; petals violet, the odd one more or less villous; cleistogamous flowers on erect or ascending peduncles, intermediate in length to those of the parent species; capsules 8–12 mm. long, infertile, averaging in 12 capsules 8¼

seeds; seeds brown, 2 mm. long; offspring notably diversiform. (PLATE 15, *Aa*.)

Several sowings have been made of the seeds of this hybrid; but the ten plants of the first brood (236), whose offspring have been raised for two succeeding generations, are the only ones that will be here discussed. The forms of leaf found in the ten plants and in their respective broods of offspring are presented in the first half of TABLE I. The second half presents the corresponding facts regarding sixteen offspring of brood 236, plant 3, whose leaf had a hybrid form, quite the same as that of the mother plant from Illinois.

TABLE I

CULTURES OF VIOLA PAPILIONACEA × PEDATIFIDA FOR FOUR GENERATIONS

V. papilionacea has leaf uncut:—*a*
V. pedatifida has leaf parted:—*A*
Their HYBRID has leaf cleft:—*Aa*

Ten F_2 offspring of hybrid

Brood 236	Leaf form	Their offspring—F_3 Brood	Number and form *A*	*Aa*	*a*	Total
No. 2	*A*	595	30			30
No. 3	*Aa*	468	6	5	5	52
		596	8	20	8	
No. 4	*Aa*	597	3	6	1	10
No. 6	*a*	598			16	16
No. 7	*A*	599	16			16
No. 8	*Aa*	600	1	10	3	14
No. 9	*Aa*	601	2	1	1	4
No. 10	*Aa*	602	6	6	3	15
No. 11	*A*	603	13			13
No. 12	*Aa*	604	3	5	2	10
Total			88	53	39	180
From *Aa*'s			29	53	23	105

Sixteen F_3 offspring of 236–3

Brood 468	Leaf form	Their offspring—F_4 Brood	Number and form *A*	*Aa*	*a*	Total
No. 1	*A*	605	12			12
No. 2	*Aa*	606	3	5	5	13
No. 3	*Aa*	607	4	6	3	13
No. 4	*A*	608	14			14
No. 5	*a*	609			15	15
No. 6	*A*	610	20			20
No. 7	*a*	611			11	11
No. 8	*A*	612	14			14
No. 9	*a*	613			16	16
No. 11	*Aa*	615	3	6	3	12
No. 12	*Aa*	616	3	7	3	13
No. 13	*A*	617	12			12
No. 14	*A*	618	12			12
No. 15	*a*	619			12	12
No. 16	*Aa*	620	2	7	4	13
No. 17	*a*	621			14	14
Total			99	31	86	216
From *Aa*'s			15	31	18	64

The cultures show that in this hybrid the Mendelian law controls in a general way the inheritance of leaf form, though there is no dominance, the hybrid leaf being intermediate between the leaves of the two parents. The plants that resemble *V. pedatifida* in having parted leaves always produce offspring with parted leaves; those that resemble *V. papilionacea* in having uncut leaves always produce offspring with uncut leaves; while those

that have the compromise leaf reproduce plants with three forms of leaf incision, as did the original hybrid. Also in the relative *number* of these forms there is an approximation to the Mendelian ratio 1 : 2 : 1. In the above 26 plants (broods 236 and 468), whose forms were verified by their offspring, there are 9 *A*'s, 11 *Aa*'s, 6 *a*'s, the theoretical ratio being: 6½ *A*'s, 13 *Aa*'s, 6½ *a*'s. In the 169 offspring of *Aa* plants, given above for the third and fourth generations, there are 44 *A*'s, 84 *Aa*'s, 41 *a*'s, the theoretical ratio being: 42¼ *A*'s, 84½ *Aa*'s, 42¼ *a*'s. Here we find, as usual, that the larger the number of individuals the closer the normal ratio is realized.

But besides general conformity there are also departures from the strict Mendelian law. For one thing the hybrid or intermediate leaf varies in different individuals, inclining now more to the form of the one parent species and now more to the form of the other. Also the reversionary forms, designated as *A* and *a*, are rarely complete reversions. The *A* plants, though stable in producing like parted leaves in succeeding generations, do not have leaves as *deeply* parted as in *V. pedatifida;* and the *a* plants, though plainly uncut and stable, usually have teeth noticeably longer than in normal *V. papilionacea*, sometimes even pectinate. (PLATE 15, FIG. *a*.)

Another cause often conspires to increase these differences in leaf pattern: the presence of minor hybrid characters that independently adjust their special conflicts of hybridity. For example, the leaf of *V. pedatifida* is usually truncate or even cuneate at the base, that of *V. papilionacea* usually cordate. A hybrid offspring may inherit the broad truncate base of the former with the uncut margin of the latter. Sometimes in the hybrid leaf the lobes are entire, and obtuse at the tip; sometimes, as in the normal leaf of *V. pedatifida*, the lobes are again cleft or toothed on the outer margin, and acute at the tip.

In these various ways there has arisen in the numerous progeny of the hybrid under discussion a considerable diversity of foliage, such as would present insoluble difficulties to a taxonomic student, who did not know that these diverse forms all came from one individual, by close-fertilized reproduction, in the short period of three or four years. The extreme differences are such as would

warrant the making of several distinct species, according to the hasty methods of ordinary practice.

The hybrid *V. papilionacea* × *pedatifida* seems not to be rare in the Middle West. I cite a few interesting examples: *M. A. Castleton 25*, Vinita, Okla., April 18, 1891; distributed as "*V. palmata*."* From the United States National Herbarium in 1911 was distributed with printed ticket: "*Viola Bernardi* Greene, Freeport, Ill., *Charles F. Johnson*, May 15, 1899; determined by Dr. E. L. Greene and Philip Dowell." The plant is quite the same as the hybrid under discussion from Yorkville, Ill., and seems to represent Dr. Greene's present conception of his species. *V. indivisa* Greene is also a derivative form of this hybrid; the "type" from Prairie Junction, Minn., *E. L. Greene* coll., July 7, 1898 (Pittonia **5**: 124. *pl. 13*. 1903). Also along railway, Naperville, Ill., *L. M. Umbach*, May 18, 1897. (Cf. Leaflets **1**: 182. 1906.)

2. Viola pedatifida × sagittata hyb. nov.

Plant becoming cespitose, the rootstock dividing into several erect branches; leaves that develop after petaliferous flowering finely pubescent especially beneath and on the upper portion of the petiole, the blades subcordate-ovate in outline (the width about ⅔ the length), cleft into 6–8 oblong-linear lateral lobes and a broad slightly toothed terminal lobe, the leaves of late summer relatively broader; petals violet, the three lower villous; apetalous flowers and fruit on erect peduncles as long as the petioles; auricles of sepals long and divergent; capsules green, 6–10 mm. long, often quite infertile; seeds intermediate to those of the two parent species in size and color; offspring much unlike each other in foliage, but blades always incised or coarsely toothed toward the base. (PLATE 16, FIG. *Aa*.)

This hybrid first attracted my attention in a parcel of violet specimens collected in central Illinois by Mr. V. H. Chase, and sent me in November 1907 for determination. It was found in undisturbed prairie soil along the right of way of the Rock Island and Peoria Railroad, just north of the south boundary of Stark County. At the same place and time were collected *V. pedatifida* and pubescent *V. sagittata*, the three plants bearing the consecutive numbers *1356–7–8*. The anomalous plant impressed me as

* Regarded as *V. viarum* by Mr. Pollard, and apparently the basis for accrediting this species to Ind. Terr. in Britton's Manual, p. 636. 1905.

distinct from *V. pedatifida* × *sororia*, discussed below, and as a cross between the two species with which it grew. Mr. Chase, to whom I appealed for living plants, found that the station had been recently burned over; but the following May he discovered another colony along the railway a half mile farther south (*V. H. Chase 1619*). The stocky specimen sent was easily divided, and six or eight vigorous plants were obtained during the season of 1908. Mr. Chase reported that the pubescent *V. sagittata* "was very abundant, thousands of plants cover the ground with a blue carpet, mostly where the land was a little low and damp. *V. pedatifida* seemed to prefer rather drier ground. The hybrid was invariably with *V. pedatifida*, on fairly dry soil; and *V. sagittata* was never more than a few rods away."

During the season of 1909 I grew nineteen offspring of *Chase 1619*, and they gave abundant evidence as to the taxonomic status of the mother plant. Leaves of nine of these offspring are figured in PLATE 16 and indicate something of the marked diversity of form resulting from the combination, in the leaf of the original hybrid, of at least four pairs of opposed characters,* that blend or segregate, independently and variously, in the several offspring.

3. **Viola pedatifida** × **sororia** hyb. nov.

Becoming cespitose with multicipital caudex; leaves that expand at petaliferous flowering 9–13-cleft, the lateral lobes broadly linear, usually with one or two coarse teeth on the outer edge toward the apex, the middle lobe much broader and incised on either side, the upper face somewhat hirtellous, the lower surface and the petioles villous; the leaves of summer larger and less deeply cleft; apetalous flowers on rather short, erect or ascending peduncles; the capsules somewhat blotched with purple, bearing 5–20 brown seeds 2 mm. long; offspring markedly dissimilar. Not rare on prairies of the Middle West. (PLATE 17.)

I am greatly indebted to the kindness and skill of Mr. Chase for the abundant and excellent material used in the study of this hybrid. Collectors in this region know that the native flora of the open prairies is now largely restricted to untilled strips of land

* These are:	*V. pedatifida*	*V. sagittata*
1. Outline	broadly flabelliform	lanceolate
2. Form of base	truncate or cuneate	cordate or subcordate
3. Incision	2–3-ternately dissected	coarsely toothed at base
4. Pubescence	margins and veins hirtellous	finely pubescent

along the borders of railways. On May 16, 1909, Mr. Chase, whose bicycle was adjusted to run on rails, traversed in 5 hours the 24 miles between his home at Wady Petra and the town of Galva. In order to make the return by train, he says, "I could not stop to *hunt* along the way; but whenever I saw a cut-leaved violet that was not *V. pedatifida* I stopped for it." The twelve numbers of living plants collected on this trip reached me safely, and all have flourished in the Vermont garden.

The status of hybrid plants in the wild is well shown by a detailed study of these specimens and of their offspring; for all but two sterile plants have been reproduced by seed. The main points regarding them, that have a bearing on the present problem of hybridism, are presented in the following tabular synopsis (TABLE II):

TABLE II

VIOLET PLANTS COLLECTED BY V. H. CHASE IN CENTRAL ILLINOIS, MAY 16, 1909

	Chase's herb. no.	Leaf characters		Capsule color	Seed color	Av. no. in one capsule
V. pedatifida Don	1951, 1956	**A** (parted)	**b** (glabrous)	**c** (green)	**d** (buff)	70
V. sororia Willd...	1291	**a** (uncut)	**B** (villous)	**C** (purple)	**D** (brown)	66
V. papilionacea Ph.	1958	**a**	**b**	**C**	**D**	66
V. papilionacea × *pedatifida*	1950	*Aa*	*b*	sterile		0
	1952	*a*	*b*	*c*	*Dd*	7
	1949	*Aa*	*b*	*Cc*	*d*	9¾
	1947	*Aa*	*b*	*Cc*	*Dd*, or *d*	5
V. pedatifida × *sororia*	1957	*Aa*	*Bb*	sterile		0
	1955	*A*	*Bb*	*Cc*	*Dd*	10½
	1953	*Aa*	*Bb*	*c*	*Dd*	7
	1954	*Aa*	*Bb*	*Cc*	*Dd*	8
	1948	*Aa*	*Bb*	*Cc*	*Dd*	18

Nos. 1951 and 1956 are *V. pedatifida;* and I have added to the list, though not collected May 16, 1909, *V. sororia*, the other parent of the hybrid under discussion; specimens of this had been previously sent me by Mr. Chase from four stations in his vicinity. No. 1958 is the prairie form of *V. papilionacea*, named *V. pratincola* by Dr. Greene (Pittonia 4: 64. Jl 1899). These three are common and widespread species of the Prairie States from Canada to Texas; the first and third reach westward to the mountains of Colorado.

Four of the numbers are the hybrid *V. papilionacea* × *peda-*

tifida, already discussed in this paper. Of these no. 1950 flowers freely in May with showy flowers, that often appear also in July and August; but apetalous flowers are rare, and neither sort has been found to produce seed. The three others are also nearly sterile, bearing only 5–10 seeds to a capsule; but none of the three turns out to be like the Pollard plant from Yorkville in being a first cross (or F_1), the form to be selected as the starting point for experiments on the laws of inheritance in hybrid offspring. No. 1952 has an uncut leaf as in *V. papilionacea* and a green colored capsule as in *V. pedatifida*, both recessive or reversionary characters never found in a first cross. No. 1949, on the other hand, has the hybrid leaf and the hybrid capsule color but the buff seeds of *V. pedatifida* and is therefore another subhybrid. No. 1947 consists of five plants, the seeds of which differ in color, and the leaves of which, though somewhat incised, display at least three unlike patterns; the five plants therefore must be considered the offspring of an earlier hybrid.

The remaining plants of the 1909 collection are equally variant forms but of *V. pedatifida* × *sororia*. No. 1957 is of dwarf habit and has the compromise or hybrid leaf; but though vigorous and multiplied by division into eleven plants, it has failed to yield a single seed. No. 1955 (six plants by division) has a leaf more deeply cut that the others, and this style of leaf reappears in all its offspring. In this we see a reversion, far from complete but stable, to the leaf of *V. pedatifida*. No. 1953 (again six plants by division) has the pure green capsules of *V. pedatifida*, as have also its offspring, and so is another subhybrid. But the two remaining numbers, 1954 and 1948, seem to be the desired first product of hybridism, all the four pairs of opposed characters in the double parentage appearing in a compromise form in both numbers. A flowering specimen of 1954 was distributed in my "violets of eastern North America, 1910," no. 121; and in no. 122 are shown two sister offspring, one with the uncut leaves of *V. sororia*, the other with the parted leaves of *V. pedatifida*.* No.

* In one of our large herbaria, where the work of mounting is done by novices, these two offspring were considered too unlike to appear on the same sheet. Only the plant with uncut leaves was mounted over ticket 122; while the sister plant with parted leaves was placed on the sheet with no. 121, which indeed it more closely resembled. That two plants so dissimilar should come from one self-fertilized parent has seemed incredible even to certain "botanists."

1948, being unusually fertile for a hybrid, was chosen for the basis of a somewhat detailed study of the reproductive behavior of a tetrahybrid.

During the season of 1910 twenty-one plants were grown from the seeds of *Chase 1948*. In August nearly all bore cleistogamous flowers, which matured several capsules of seeds. These were sown about December 1 in shallow boxes and placed in a cold frame with no protection from the winter weather but a covering of burlap. In the spring of 1911 all but seven of these sowings gave broods of F_3 offspring, containing each 6–18 plants. These have been carefully observed for two seasons and the characters of each plant noted as respects leaf incision, pubescence, color of capsule, and color of seed, four qualities in which the parent species were opposed. In each of these four qualities the plant resembled either *V. pedatifida*, *V. sororia*, or their hybrid; and in most instances the data were at hand, and clear enough, to determine at once this resemblance by inspection. In the case of the sixteen F_2 plants of brood 781, here made use of, the characters were verified by the behavior of their offspring, the reversionary forms always proving stable, the hybrid forms always unstable. The details of this experiment are given in TABLE III, in which the symbols *Aa*, *Bb*, *Cc*, *Dd* denote the blend or hybrid character.

The statements made above regarding the marked diversity of leaf pattern in the offspring of *V. papilionacea* × *pedatifida* and the departures from strict Mendelian law are equally true of the analogous hybrid *V. pedatifida* × *sororia*. The imperfect reversions in leaf form are shown in PLATE 17, FIG. *A.B*, *A.Bb*, and *A.b*, compared with the leaf of *V. pedatifida* figured above them. But in this hybrid the same phenomena are observable also in the varying colors of capsule and of seed. In all three pairs of characters the stable reversions marked *A*, *C*, and *D* are not complete reversions. The darkest capsule or seed found in the F_2 brood is much lighter than the capsule or seed of *V. sororia*.

It is further to be observed that though the Mendelian law leads us to expect on the average one of each of these reversions in every four offspring, we have here only one of each in the *sixteen* offspring. At the same time the *hybrid* forms are in excess of the

normal average (one half of the whole number); instead of 8 of each we have 10 *Aa*'s, 12 *Cc*'s, and 10 *Dd*'s. And it should be remembered that this statement is not based solely on the appearance of the F_2 plant but on the fact that the reversionary characters, *A*, *C*, *D*, were found to be stable in reproduction; while the hybrid characters were found to be unstable. For example, with the exception of no. 4, which had only two offspring, each of the ten *Aa* plants in brood 781 gave 2–7 plants with uncut leaves.

TABLE III

VIOLA PEDATIFIDA × SORORIA, CHASE 1948, AND ITS OFFSPRING

Hybrid F_1	*Aa*	*Bb*	*Cc*	*Dd*			
Forms of sixteen F_2 offspring					F_3 offspring of brood 781		
Brood	Foliage		Capsule	Seed	Brood	Size	Exhybrids
781 no. 1	*a*	*B*	*Cc*	*d*	853	13 plants	8 { 5 *a.B.C.d* 3 *a.B.c.d*
781 no. 3	*a*	*B*	*Cc*	*d*	855	10 plants	7 { 2 *a.B.C.d* 5 *a.B.c.d*
781 no. 4	*Aa*	*Bb*	*Cc*	*Dd*	856	2 plants	0
781 no. 6	*A*	*Bb*	*Cc*	*Dd*	858	16 plants	3 { 1 *A.B.c.d* 1 *A.b.C.d* 1 *A.b.c.d*
781 no. 7	*Aa*	*b*	*Cc*	*Dd*	859	7 plants	0
781 no. 8	*Aa*	*B*	*C*	*d*	860	6 plants	4 { 2 *a.B.C.d* 2 *A.B.C.d*
781 no. 9	*Aa*	*B*	*Cc*	*D*	861	16 plants	3 { 1 *A.B.C.D* 1 *A.B.c.D* 1 *a.B.c.D*
781 no. 10	*Aa*	*b*	*Cc*	*Dd*	862	14 plants	1 *a.b.c.D*
781 no. 11	*Aa*	*Bb*	*c*	*Dd*	863	11 plants	2 { 1 *A.b.c.d* 1 *a.b.c.d*
781 no. 13	*a*	*Bb*	*Cc*	*Dd*	865	2 plants	0
781 no. 14	*a*	*B*	*c*	*Dd*	866	9 plants	6 { 3 *a.B.c.D* 3 *a.B.c.d*
781 no. 15	*Aa*	*Bb*	*C*	*d*	867	15 plants	1 *a.B.C.d*
781 no. 16	*Aa*	*Bb*	*Cc*	*Dd*	868	10 plants	0
781 no. 17	*Aa*	*Bb*	*Cc*	*d*	869	18 plants	2 { 1 *a.B.C.d* 1 *a.B.c.d*
781 no. 19	*a*	*b*	*Cc*	*Dd*	871	8 plants	1 *a.b.c.d*
781 no. 20	*Aa*	*b*	*Cc*	*Dd*	872	14 plants	3 { 1 *A.b.C.d* 1 *A.b.c.d* 1 *a.b.c.d*
						171 plants	41

And not only in the second but also in the third generation of this hybrid the number of plants having the positive character seems to fall short of the Mendelian requirements. This appears if

we note the ratio in which the several hybrid characters in brood 781 segregate in the F_3 offspring:

The 10 *Aa* plants had 113 offspring:	23 *A*'s, 54 *Aa*'s, 36 *a*'s	ratio in %	20:48:32
The 7 *Bb* plants had 74 offspring:	14 *B*'s, 35 *Bb*'s, 25 *b*'s		19:47:34
The 12 *Cc* plants had 130 offspring:	23 *C*'s, 67 *Cc*'s, 40 *c*'s		18:51:31
The 10 *Dd* plants had 93 offspring:	13 *D*'s, 44 *Dd*'s, 36 *d*'s		14:47:39
Total 410	73	normal ratio:	25:50:25

Combining these results, we find in 410 instances of the reproduction of a hybrid character, that instead of 102½ reversions to the positive character there are only 73; instead of 25 per cent, only 18.

However, the determination of the characters in these 171 F_3 offspring rests only upon their appearance, having not been as yet verified by observing the behavior of the F_4 offspring. Of this generation 45–50 broods are hoped for by another season from seed already sown. But we seem to be already justified in the suspicion that in a species-hybrid as complex as the one under experiment, where the opposed characters of the parents appear in a blend or intermediate form, this form may acquire a certain degree of fixity, whereby the reversions to the positive type in a pair of opposed characters are less complete and less frequent than in normal Mendelian segregation and the reversions to the negative type more frequent. If we might assume that the gametes holding the positive character were more or less impure, while the gametes holding the negative character were pure, the situation would be fairly well accounted for.

In the great diversity of forms displayed in the 171 F_3 offspring the most interesting group are the 41 exhybrids, in which all of the four characters under study are reversionary and constant. Among these we find three plants in which the four characters of *V. pedatifida*, *A.b.c.d*, reappear, one plant in each of the broods 858, 863, and 872. What may be called a form of *V. pedatifida* with uncut leaves, *a.b.c.d*, is found once in each of the broods 863, 871, 872. A pubescent *V. pedatifida*, *A.B.c.d*, occurs in brood 858. A purple-capsuled *V. pedatifida*, *A.b.C.d*, occurs in both 858 and 872. Similarly, we have a cut-leaved *V. sororia*, *A.B.C.D*, in brood 861; a green-capsuled *V. sororia*, *a.B.c.D*, once in brood 861 and three times in brood 866; and a buff-seeded *V. sororia*, *a.B.C.d*, in broods 853, 855, 860, 867, and 869, eleven plants in all. In short, all but five of the sixteen possible combi-

nations in fours, of these eight pure elementary characters, are to be found in these 41 plants.

As showing how a hybrid tends in successive generations to eliminate its hybrid characters, ever becoming simpler and finally pure, we note that starting with the F_1 plants, necessarily hybrid in all the opposed characters of the two parent species, we have in the next generation only two such hybrids, and in the 171 plants of the 3d generation, none; indeed, the law of probability calls here for only one in every 256 offspring.

My first recognition of *V. pedatifida* × *sororia* was in a package of living plants sent May 22, 1907, by Dr. H. V. Ogden of Milwaukee, collected at Upper Nemahbin Lake, Wis., growing with both parents, and considered by him as "doubtless a hybrid." The same thing, however, had been sent me some three years earlier by Dr. Greene as a specimen of his *V. Bernardi*, collected by himself at Dixon, Ill., June 18, 1898. In Leaflets 1: 184. Ja 1906, the plant is transferred to *V. perpensa*, then first described. I have recently examined the three other specimens there cited and regard them all as forms of *V. pedatifida* × *sororia*.* Also *V. fallacissima* Greene, Leaflets 1: 185. Ja 1906, is another form of the same hybrid from western Missouri—*Bush 141*, Lee's Summit, Mo., July 8, 1899. Other specimens are: *E. J. Palmer 3345 and 3393*, Webb City, Mo., April 19 and May 5, 1911; *Mary O. Pollard 6*, Yorkville, Ill., May 16, 1909; *L. M. Umbach*, prairies, Clarendon Hills, Ill., June 21, 1899—distributed in 1911 from United States National Herbarium as "*V. palmata*."

4. **Viola nephrophylla** × **pedatifida** hyb. nov.

V. Wilmattae Pollard, Proc. Biol. Soc. Wash. **15**: 178. Au 1902†

Foliage much as in *V. papilionacea* × *pedatifida*, nearly glabrous, palmatifid with several narrow lateral lobes; corolla "deep violet, 2 cm. broad"; petals markedly villous and sepals with slightly scarious margins, as in *V. nephrophylla*.

It has not been practicable to secure living plants for cultures. But the alleged parent species were both growing in the cañon,

* I therefore wish to correct my statement in Bull. Torrey Club **37**: 584. 1910 that *V. perpensa* Greene is the western form of *V. palmata*—a too hasty inference from the fact that a *V. palmata* specimen in my herbarium from Aurora, Ill., was once named *V. Bernardi* by Mr. C. L. Pollard.

† The type is 404,924 United States National Herbarium, *Mrs. Wilmatte P. Cockerell*, Sapello Cañon (c. 8000 ft. alt.), Beulah, New Mex., May 5, 1901.

and the status of the plant is strikingly analogous to that of numbers 1 and 3 above described. The supposed hybrid has been recently again collected, by Mr. Paul C. Standley.* The leaves in his specimens are cut about halfway to the midrib; but on the same sheet are two detached leaves parted as in *V. pedatifida*, indicating that this species grew with the anomalous plant.

MIDDLEBURY, VERMONT

Explanation of plates

PLATE 1

Figures ½ natural size

Aa. Viola papilionacea × *pedatifida* Brainerd, transplanted, May 1905, from Yorkville, Ill., *Mary O. Pollard* coll.; ex horto Middlebury, Vt., May 14, 1910. No. 109 Brainerd's violets of eastern No. Am., 1910.

A. F_4 offspring of Aa, having stable leaf pattern resembling that of *V. pedatifida*; ex horto (brood 612) Middlebury, Vt., June 2, 1912.

a. F_2 offspring of Aa, having stable leaf pattern resembling that of *V. papilionacea;* ex horto (brood 236 plant 6) Middlebury, Vt., June 3, 1909.

PLATE 2

Figures ½ natural size

A. Leaf of *Viola pedatifida* Don, south of Wady Petra, Stark Co., Ill., *V. H. Chase 1356*, May 26, 1907.

a. Leaf of pubescent *V. sagittata* Ait., south of Wady Petra, Ill., *V. H. Chase 1524*, July 28, 1907.

Aa. Viola pedatifida × *sagittata* Brainerd, transplanted, May 3, 1908, from along railway 1¼ miles south of Wady Petra, Ill., *V. H. Chase 1619;* ex horto Middlebury, Vt., Sept. 7, 1909.

1–13. Characteristic leaves of nine F_2 offspring of above hybrid; ex horto (brood 630) October 1909.

PLATE 3

Figures ½ natural size

A leaf of *Viola pedatifida* Don, transplanted, May 1909, from near Galva, Ill., *V. H. Chase 1951;* ex horto (brood 851) Oct. 3, 1911.

A leaf of *V. sororia* Willd., transplanted, May 1909, from Yorkville, Ill., *Mary O. Pollard* coll.; ex horto (brood 707) Aug. 31, 1910.

Hybrid leaf of *V. pedatifida* × *sororia* Brainerd, transplanted, May 1909, from along railway, Stark Co., Ill., *V. H. Chase 1948;* ex horto Aug. 31, 1909.

A.B.—a.b. Characteristic leaves of nine offspring of this hybrid, viz:

A.B, F_2, plant 1 of brood 861, stable as to pubescent palmatifid leaf.
Aa.B, F_2, plant 9 of brood 781, stable as to pubescent leaf only.
a.B, F_2, plant 14 of brood 781, stable as to pubescent uncut leaf.
A.Bb, F_2, plant 8 of brood 868, stable as to palmatifid leaf only.
Aa.Bb, F_2, plant 17 of brood 781, hybrid in both pubescence and form of leaf.
a.Bb, F_2, plant 8 of brood 867, stable as to uncut leaf only.
A.b, F_4, plant 9 of brood 995, stable as to glabrous palmatifid leaf.
Aa.b, F_2, plant 7 of brood 781, stable as to glabrous leaf only.
a.b, F_4, plant 0 of brood 998, stable as to glabrous uncut leaf.

* United States National Herbarium, *Standley 6072*, near the Sierra Grande 2100–2925 m. alt.), Union Co., New Mex., June 18, 1911.

Viola obliqua Hill and other violets

EUGENE P. BICKNELL

Viola obliqua—the name is become anathema! Venerable indeed, yet from of old misunderstood even by those who have sought to do it honor, rejected, reinstated, and at last altogether cast out, it may be deemed a matter for apology that it should be now once again brought forward. Nevertheless I ask a further hearing in its behalf—the fraternity of violarians must be my judge.

The name seems first to have emerged into the modern light in the Illustrated Flora. If recollection be not at fault, I myself had some part in this. And the view then shared with the author of that work, Hill's illustration before us, that this discredited name was perfectly available for exact use, has not suffered any change. I have not turned to Hill's much ridiculed plate from that day until this writing, nor do I suppose that Doctor Britton has, yet, viewing it together now we are at agreement as before.

More redoubtably than any other writer, more picturesquely, Doctor Greene has used his slings and arrows against this name.* Yet, as his page presently allows us to see, with friendly purpose! His onslaught—assuredly not to be withstood—finally by a hairsbreadth evades a fatal issue. With fine dexterity the all but destroyed thing has been rescued and, on the instant, sent forth with now well-established rights—for how shall it ever again be assailed with better success? Yet somewhere was a miscalculation. Later writers, and there have appeared not a few, have approved the name as extinct, perhaps not stopping to apprehend this reinstatement or the dryness of Doctor Greene's closing avowal " the most common of all East American violets . . . I am confident it can never be proven that it is not *Viola obliqua* Hill."

Doctor Greene has made his hypothetical objector say of Hill's plate that " it does not half represent any violet that ever grew in any country. It is glaringly false in representing flowers erect on

* Pittonia 3: 142–143. 1896.

peduncles perfectly straight to the very summit." Thus is the overtechnical critic at first gaily allowed his fling. But this imagined sceptic need have made less allowance for the "unbotanical draughtsman" than it is implied he should have done. Had Doctor Greene's keen eye ever scanned the woodland floor among the hills along the Hudson, or on Long Island, it must have seen in apparition before it this same pictured violet of Hill's side by side with its living counterpart having flowers postured in the self same upwardly oblique way and even strictly erect! Here then was the living vindication of *Viola obliqua* Hill and Sir John had waited nearly a century and a half to be put in credit. The surprising thing is that his figure ever should have come under any doubt. It utters authenticity. Its entire composition proclaims that it could have been in no part extemporized. Beyond peradventure we see in it the copy of an actual plant worked over by a conscientious but not a facile draughtsman. No inattentive sketch, no artist's fiction, would have been cumbered with the needless and inartistic detail shown in this cut nor, like it, reveal the painstaking effort of a careful but none too practised hand. Nor, as to the flowers should it have been forgotten that Hill put in print, and he had the living plant, that they were "oblique," and Aiton that they were "erect." I do not know whether this violet remained in cultivation in England up to the time when Aiton wrote or whether he had ever seen it in growth. But if his description was drawn up from herbarium specimens having the petals partly discolored from drying it offers an explanation of his use of the word *straminea* in giving the color of the flowers. By fault of this word, nothing else can explain it, the history of the blue-flowered *Viola obliqua* has come confusingly in touch with violets so remotely related to it as the white- or creamy-flowered *Viola blanda* and the yellow-flowered *Viola rotundifolia*.

As for our plant which so perfectly upholds Hill's illustration I doubt not that it may be found bearing its upwardly looking flowers over a far wider range than where I myself have seen it growing, for it is none other than the common violet we have been taught to call *Viola affinis* LeConte. The Illustrated Flora was therefore right in restoring the name *Viola obliqua*, although

not drawing the specific lines so closely as we may now do; Doctor Greene was right in supporting the name with his endorsement; Mr. Pollard in Britton's Manual was exactly right in allowing Hill's name to displace LeConte's. Notwithstanding all this the name *Viola obliqua* will be searched for in vain in the violet writings of the day.

The plant figured by Hill was not that extreme form of the species of slighter figure and narrower leaf that we seem to have set up as typical of *Viola affinis*. But it was of the same flexuous habit, the same grouping of foliage and flower, the same deep cordation and acuteness of the expanded leaf; the blades had the same pronouncedly crenate-serrate marginal pattern, and some of them were quite sufficiently narrow and attenuate to satisfy the most exacting *affinis* standard. It is no objection that other leaves were broadly ovate. Forms of the species, very usual forms, do produce just such broadly ovate leaves and in like way associated on the same plant with the more characteristic narrower ones. Such plants, and others much more strongly grown than the medium plant portrayed by Hill, are not possibly to be kept distinct by a name from the most reduced and delicate forms of the series, for the extreme phases are everywhere inextricably blended together through every avenue of intergradation.

It must not be inferred that there is a particular form of *Viola obliqua* in which the flowers at some stage of their growth always become upturned. This trait of the flower is no more than a tendency in the general species which, in some plants, or colonies of plants, may be perfectly realized, while in others it is not seen at all or proceeds no further than an opening out of the crooked tip of the peduncle causing the flower to stand away from the scape in a horizontal or an upwardly oblique position just as it may in many another violet. Nor is the erect position of the flower at all extraordinary among violets. It is occasionally seen in other species although in no other known to me does it come to a well-established trait, and in no other than this, except rarely, have I seen the flowers strictly "erect or peduncles perfectly straight to the very summit."

Just as our medium plant passes down into its smaller and more delicate forms so also, and with as gradual transformation, does it grow up into an every way larger violet having thicker

leaves, obtuse and of less pronounced crenation, and more striking flowers of deeper hue and bluer tone of color. Of late years much has been made of this larger violet, and forms which cluster about it, under the designation *Viola papilionacea* Pursh.

Let us digress upon this rather ostentatious newcomer among our named violets. For myself I have never quite succeeded in finding out what was the touchstone of "*Viola papilionacea*." Nor does there appear to be perfect accord among its sponsors as to its exact credentials. Mr. Pollard in first taking up the name* introduced us to a wholly glabrous plant, describing accurately the fine violet to which we have just adverted. But the specimens he put out† were at some discord with his description, showing us a violet having a characteristic pubescence on the petioles. In respect of this pubescence the specimens coincide with Doctor Greene's understanding of "*papilionacea*"‡ and with the admirable drawing of Mr. Holm which supplements his description. Mr. Stone, both by description and illustration, reports the plant as bearing pubescence on the petioles.§ Mr. House as well.‖ Doctor Brainerd, on the other hand, although taking a broader treatment, seems more in accord with Mr. Pollard in his description of a wholly glabrous plant** as also is Doctor Dowell††—something like an even division between the smooths and the roughs. All this is not making too much of a little pubescence, for the glabrous and the pubescent plants differ by far more than this one character. And the strain of discrepancy running through the discussions of "*papilionacea*" is reason enough why this conjectural species has not been received by all of us with any such compelling sense of recognition as, for instance, all felt towards "*Viola cucullata*" the instant that Doctor Greene gave us the cue.

The glabrous "*papilionacea*" is found on grassy banks or at the borders of meadows along descending places from woodlands

* Bot. Gazette **26**: 136. 1898.

† North Am. Violaceae. Determined and distributed by Prof. Edward L. Greene and Mr. Charles Louis Pollard, No. 8.

‡ Pittonia **4**: 140–141. 1900.

§ Proc. Acad. Nat. Sci. Phila. **55**: 670–671. 1904.

‖ Bull. Torrey Club **32**: 258. 1905.

** Rhodora **6**: 15. 1904; Bull. Torrey Club **3**: 590. 1910.

†† Bull. Torrey Club **37**: 164. 1910.

where *Viola obliqua* grows. In these near meadows or by brooks that traverse the same woodlands "*Viola cucullata*" raises its long-stemmed flowers of twofold blue. In many ways the smooth "*papilionacea*" is strikingly intermediate between these two plants. Doctor Brainerd has opened our eyes to violet hybrids. Have we not found one here? I recall all these violets as they grew in profusion about my former home on the Hudson and seem to see, I did not see it then, our woodland and our meadow violet meeting in such places as I have described and crossing over into each other—how else than through free hybridization? And the perplexing intermediate examples that I had then tried to sort into species seem, as the specimens are turned to now, to lend strong confirmation to such an hypothesis. If, then, we have indeed here come upon the truth, our "*papilionacea*" is seen to be not all that we have been asked to believe. Yet by this very reduction it takes a clearer outline as a plant marked by a characteristic hairiness on the convex side of the petiole, often localized just below the blade, but often, also, thinly diffused on the lower surface of the lamina, precisely as Mr. Holm's drawing so faithfully portrays. The upper face of the blade is by no means always glabrous, but what pubescence may later appear there is not often very obvious. By this at first strictly dorsal pubescence it is a marked plant, for it should be noted of the glabrous "*papilionacea*"—whether the hybrid, if so it proves to be, or the enhanced *Viola obliqua*—that the slight pubescence it may sometimes show has its site on the upper surface of the blade just where we find evidences of it in the nearly glabrous *Viola cucullata*. It is a marked plant also, in its group, by deeply cordate and crenate-dentate leaves which in age so open out their cordation as to become subtruncate at the base, and it is an especially noteworthy violet by reason of a ready tendency to semi-domestication.

It will be well here to turn to yet another one of our violets, the pubescent *Viola sororia* Willd. In woodlands wherein this species and *Viola obliqua* are in free growth together they may be found, it is no uncommon thing, blending the one into the other in perfect confluence. Among these plants of mixed strain we recognize, now *Viola obliqua*, changed only by the beginnings of

pubescence, now its too intimate associate, still to be called *Viola sororia* but taking a more gracilent habit and narrower form of leaf. More intermediate in the series are plants of stronger growth and in these we seem to see our pubescent "*papilionacea*," never, perhaps, exactly as we know it in its semi-domesticated state but so much the same that the origin of our plant would seem to be disclosed as though in an open book. We have been here freely following appearances and may have been easily mislead in thus seeming to have traced our plant back to the mode of its beginning. Nothing like demonstration has assured us. But, if it were indeed a proved thing, even then our semi-domesticated "*papilionacea*," far along in its generations, would be manifestly of a higher category than those chance hybrids we seem to come upon in the making. Our plant thrives in places whence both of its suggested parents have disappeared, or perhaps have never been. It is become independent of the parental aid, is self perpetuating. It is, by continuous descent from season to season, no longer a hybrid, but rather a species whose hybrid origin goes back —how far we may not know. Such a plant is surely to be accorded its own distinctive name. I have not found that such a name has ever been given unless the pleasing one *Viola laetecaerulea* of Doctor Greene may happily prove to be available.

Most certainly we cannot continue to call this plant *Viola papilionacea* Pursh. We turn to Pursh and read under this name, it is so clear we cannot be mistaken, the quite sufficient description of no other violet than our common one of boggy meadows and wet places that we have been calling *Viola cucullata* Aiton. Of this violet there is an open meadow form, it has doubtless been remarked by all of us who have given any field attention to violet matters, that has definable points of difference from more usual phases of the plant and this, may we not say unmistakably, is the form more particularly held in view by Pursh. In my collections formerly made about Van Cortlandt Park I find specimens of this plant put aside as far back as 1895 under a herbarium name given with reference to the notably triangular cordate and acute leaves well-developed as early as the time of flowering. The leaves are not strongly cucullate nor strictly glabrous nor is their marginal pattern at all pronounced ("*triangu-*

laricordatis acutis crenatis subcucullatis glabriusculis"—Pursh's description could scarcely be more exact); the peduncles, at flowering, little if at all surpass the leaves in height (*pedunculis longitudine foliorum*); the flowers, compared with those of the *Viola obliqua* series, are explicitly more papilionaceous, allowing for the fanciful application of this adjective to the flower of a violet, ("*petalis obovatis: 3. inferioribus infra medium barbatis conniventibus, 2. superioribus reflexis*").* Point by point Pursh's description meets the distinctive characters of this plant, proving slightly inexact only in respect of the variable bearding of the petals, for the odd one, although sometimes slightly bearded, is prevailingly glabrous. The bearding dusted with pollen readily becomes Pursh's "yellow down." "Flowers blue, elegantly striated," points with unmistakable indication to the flowers of our meadow violet distinguished above all others by the delicacy and sharp beauty of their dark penciling. "In wet places" would scarcely be particularly affirmed of any other blue-flowered heart-leaved violet, although Pursh does say of his other one "In grassy wet places," wherein, however, is more of a distinction than might appear to one not well knowing our violets in the places where they grow. Upon the face of the evidence this other violet of Pursh's, his "*Viola cucullata* Ait.," was our *Viola obliqua*. Its glabrous leaves, cucullate only at the base, had more prominently indentured margins than the crenate leaves of his *Viola papilionacea*, he expressed the difference by calling them "serrate"; the scapes were shorter, an essential distinction; the petals were obliquely bent, therefore the upper pair less characteristically reflexed and the others more open. The two plants are thus placed by Pursh in unmistakable apposition. The lateral petals are described as being merely "bearded," not, as in his *papilionacea*, "*infra medium barbatis*," an acute distinction, not to bear a too literal rendering, but quite true in the sense that the bearding in the one species is more restricted and relatively more basal on the petal than in the other. Mr. Stone is, I think, the only recent writer who has called attention to the more forward extension of

* It should be said that this description applies more particularly to the flower in its earlier and its later stages—I know of no violet the flower of which at the stage of fullest development is not more or less widely expanded.

the bearding in *Viola obliqua*—his *Viola affinis*.* "Flowers blue, white at their base," points also to *Viola obliqua* for, while the *petals* of all these violets are white at their base, the *flowers* of this one are lighter towards the throat where those of our "*cucullata*" are characteristically of deeper hue, often in sharp contrast with the pale blue surrounding parts.

It is not to be believed that Pursh did not know both of these common violets, and I have been at pains to determine and to lay stress upon each of his described species the better to emphasize the identity of his *Viola papilionacea*, for it would appear that by right of priority this is the true name of our meadow violet that we have been miscalling *Viola cucullata* Ait.

If a decade and more ago we knew as much about our violets as we know today, however scant our present knowledge may be, Aiton's *Viola cucullata* would scarcely have been construed in terms of our meadow violet that, as we have just seen, Pursh called *Viola papilionacea*. Doctor Greene in pointing out to us this distinct but long hidden species did not adopt for it a doubtfully applicable name without using a deliberate mark of interrogation.† However unmistakable the description of any later author may be, there is not one word by Aiton himself that can be deemed distinctive of this plant. Quite otherwise. His *Viola cucullata* had, for instance, subterete scapes shorter than the leaves, which were attenuate at the apex, and the petals, the upper pair not being reflexed, were white at their base. His entire description differs in no essential from the description of Hill's *Viola obliqua*, nor does it fail at any point to apply to that plant. That species must have been the very one he had before him but, believing Hill's plant to be characterised by erect flowers, partly stramineous in color like some of the European species, he very naturally considered his own plant to be distinct by reason of blue inverted flowers on scapes reflexed at the apex, which characters, although common to all violets, he is particular to report. Can it be doubted that the name *Viola cucullata* Aiton is but a synonym of *Viola obliqua* Hill and that our meadow violet that we have allowed to bear Aiton's name should now inherit from Pursh the name *Viola papilionacea?*

* Loc. cit., p. 671.

† Fittonia 3: 143. 1896.

Yet another violet should here receive a word. Little recognition has been accorded to *Viola domestica*. I ask myself, Can it be alone from force of first impressions that this violet remains to me one of the most individualized and set apart species of its group? No other one is altogether glabrous. I have given the closest scrutiny to very many growing plants and failed to detect on even one so much as a single hair. Rare examples viewed by lens do show some obscure appressed spiculae near the margin of the leaf on its upper face, but such plants are so unusual as to suggest some admixture in the strain. By this rather remarkable absence of pubescence this violet is at marked variance from the one that has been combined with it under "*papilionacea*," in which some dorsal hairiness on the leaf is so constant a character. There is other evidence that these two violets are of collateral rather than lineal relationship. In more than one direction they disclose an obviously different course of growth. In the pubescent one, I know not what other name to call it by than *Viola laetecaerulea* Greene, the scapes at flowering are erect, bearing the flowers high, even above the leaves, later becoming flexuous or sometimes declined; in *Viola domestica* they are always shorter than the leaves and tend to rise obliquely, sometimes bearing the flowers out around the sides of the tuft. The light green leaves of *Viola laetecaerulea* at flowering time are normally deeply cordate, later becoming dilated and taking a more or less subtruncate base; those of *Viola domestica* are from the first openly cordate or subtruncate and show much less change of form with age. They are of a strikingly bright deep green and when young somewhat succulent and shining. The flowers are unlike those of *Viola laetecaerulea*, or any other violet known to me, having longer more twisted often narrowly rhomboid petals of deeper hue intensifying into a dark true purple. The upper pair when in ultimate position are not only reflexed but deflexed backward by a downward twist from the base. *Viola laetecaerulea* is one of our earliest flowering blue violets, *Viola domestica* the latest of all. While the former is partly domesticated the latter must be, I think, considered as wholly so. It is found by fence rows, in old orchards, yards and abandoned grounds, growing in rich but never in wet soils and in shade or partial shade as if it had come originally from

the woods. But I have never found it in a really wild state, that is to say, never far away from the habitations of man. It is of more gregarious habits than any of our wild species, often colonizing so thickly over wide spaces as to crowd out most other plants and, until taking its strong later growth, is low and somewhat spreading of leaf and peduncle, keeping close to the ground; not least to be noted is its relatively narrow range of variation, which is unusual among the violets of its immediate relationship. It has been classed with "*papilionacea*", although its nearest ally is doubtless *Viola obliqua;* but it is too signally different from that species to be forced upon it. Because hybridization may have at some period entered into the history of *Viola laetecaerulea*, of domestic tendencies, there might be reason for inquiring whether *Viola domestica* had not a like origin, but, if *Viola obliqua* is or was one parent, where is the other?

Should the indications reported in this paper not be mistakenly understood the facts before us would be these: That the name *Viola obliqua* Hill belongs to the common and widely variable violet that we have been calling *Viola affinis* LeConte. That no such species exists as the supposed one we have been calling "*Viola papilionacea,*" this being a mixture, partly an accentuated phase of *Viola obliqua*, partly a hybrid of that species with our meadow violet, partly also a cross of *Viola obliqua* with *Viola sororia* and partly a well appointed violet, perhaps descended from such a cross, which may be called, pending proof, *Viola laetecaerulea* Greene. That the *Viola cucullata* of Aiton is a synonym of *Viola obliqua* Hill, and that our meadow violet that we have known as *cucullata* was first described by Pursh, receiving the inalienable name *Viola papilionacea*. That *Viola domestica* is, by attributes of form and habit, invested with a signal individuality and that notwithstanding its domesticated nature the source of its origin does not yet appear.

NEW YORK

Observations on the inception, season, and duration of cambium development in the American larch [Larix laricina (Du Roi) Koch.] *

L. KNUDSON

(WITH PLATES 18 AND 19)

INTRODUCTORY

During the past twenty-five years very little attention has been devoted to a minute study of the diameter increase in trees. Comparatively little is known concerning the season of wood formation; and with respect to the region of the tree in which diameter increase first begins, the evidence is contradictory. With the object of determining the part of the tree in which cambial activity begins, as well as to determine the season of growth, investigations were begun during the season of 1909 and continued in 1911. The results obtained from the study of material collected these two seasons form the basis of this paper.

The subject was suggested by Prof. W. W. Rowlee, and to him, as well as to Prof. B. M. Duggar, the writer is indebted for helpful suggestions.

HISTORICAL

The work of von Nordlinger, Th. Hartig, Robt. Hartig, Mer, and others has thrown some light upon the extent and duration of cambial activity. They have found, in general, that under forest conditions growth first begins in the youngest twigs and then proceeds downward into the older regions. Less work has been done on the cambial activity in isolated trees.

Concerning the region of first cambial activity, Th. Hartig† concluded that it occurred in the youngest twigs and then gradually extended downward. In a 30-year old *Pinus sylvestris*, and also in oak, cambial activity began almost simultaneously over the entire trunk, while in larch and maple of the same age cambial

* Laboratory of Plant Physiology, Cornell University, Contribution No. 8.

† Hartig, T. Anatomie und Physiologie der Holzpflanzen, 368. 1878.

activity began from two to four weeks later in the lower part of the trunk than in the twigs.

As a result of extensive investigations, Robt. Hartig* advanced the idea that cambial awakening was dependent upon temperature and that therefore the thickness of the bark, temperature of the soil moisture, and insolation, were important factors. He found in an isolated 10-year old *Pinus sylvestris*, that cambial activity had begun two weeks earlier than in isolated 35- and 65-year old trees, and four weeks earlier than in a 100-year old tree grown under forest conditions. The comparisons were all made at a height of 6 meters. He also found that under natural forest conditions the growth of the annular ring of Scotch pine, Norway spruce, and European larch at a height of 27.5 meters, was on June 9 respectively 66 per cent, 56 per cent and 75 per cent completed. Going toward the base the growth decreased, and at a height of 1.5 meters the percentage of the annular ring completed was 35, 21 and 18 per cent respectively. In isolated trees of Scotch pine and Norway spruce the growth on July 9 was approximately the same in all parts of the trunk. Under forest conditions growth was found to begin in the twigs and proceed downward, the cessation of growth following the same order.

According to Mer,† the cambial activity in oak, beech, basswood, fir, and other trees of twenty-five years of age and under begins in the youngest twigs. In older trees cambial activity is described as simultaneous at the bases of the branches and trunk. He states also that in a single cross-section cambial activity may be evident on one side and not on another.

Hastings‡ found that in broad-leaved trees increase in diameter did not begin until the buds had opened. He found that growth first begins in the 1-year old twigs, and later it occurs in 2- and 3-year old twigs. When wood is forming in 5- or 6-year old growth there is simultaneous development over the entire tree. In pine it begins first in the 2- and 3-year old twigs. In the hemlock the growth was first observed in the 6-year old twigs,

* Hartig, R. Das Holz der deutschen Nadelwaldbäume, 35–38. 1885.

† Mer, E. Sur les causes de variation de la densité des bois. Bull. Soc. Bot. France **39**: 95–105. 1892.

‡ Hastings, G. When increase in thickness begins in our trees. Science II. **12**: 585. 1900.

while in *Taxodium distichum* the same conditions prevail as in the broad leaves.

Buckhout* made during a period of four years caliper measurements of European larch at intervals of five days during the growing season. The measurements were made at breast height and the age of trees experimented upon is given as 45 years. He found that the formation of leaves was coincident with the beginning of diameter increase. The beginning of this increase was close to April 25, during the four years. He found a gradual increase from this date until about July 1, when further growth in diameter practically ceased. The data secured from this method of measurement are not, as he himself realized, entirely conclusive, on account of the errors which may result from the swelling and shrinking of wood and bark with the varying moisture content.

From the horticultural side gross investigations have been made by Keffer,† Goff,‡ Cranefield,§ and others on the duration of growth in fruit trees. Their work is concerned with the development of shoots and on the duration of wood increase as determined by the readiness with which the bark could be peeled. The work of these men will be considered in a subsequent paper.

METHODS OF INVESTIGATION

For the investigation during 1909, four larch trees of approximately thirteen years of age were used. These trees are hereafter designated for convenience as trees *A*, *B*, *C*, and *D*. The trees originally grew in a swamp in Oswego County, New York, but were transplanted in 1902 to the nursery on the Cornell University Campus, on land which slopes gently to the west and is of a well-drained, heavy clay soil type. The trees were planted four feet apart and were shaded on the east and west sides but not on the

* Buckhout, W. A. The formation of the annual ring of wood in European larch and the pine. Forestry Quarterly **5**: 259–267. 1907.

† Keffer, C. A. The early growth and training of apple trees. Tenn. Agr. Exp. Sta. Bull. **14**: 1–16. 1901.

‡ Goff, E. S. The resumption of root growth in spring. Wisconsin Agr. Exp. Sta. Ann. Rep. **15**: 220–228. 1898.

§ Cranefield, F. Duration of growth period in trees. Wisconsin Agr. Exp. Sta. Ann. Rep. **17**: 300–308. 1900.

north or south. Trees *B*, *C*, and *D* were very uniform as regards size and form. Tree *A*, although of the same age, was slightly smaller.

In order to determine the region of growth inception it was necessary to take material from the apex of the tree to the base. The larch has, at intervals, whorls of branches, the number of which agree approximately with the age of the tree. The trees used had each ten such whorls and material was removed from below each whorl, at different times throughout the growing season. Cuttings were made only from the south side of each tree. The first cuttings were made a few inches below each whorl of branches and the subsequent cuttings were made a few inches below the preceding and a little to one side. In obtaining the material for study two incisions, 2 cm. apart, were made through the bark and into the wood to a depth of 1 cm. and the piece then removed with a small knife. The injured area was then filled with grafting wax.

The material collected from trees *A* and *B* was fixed in a solution consisting of 33 parts glycerine, 35 parts alcohol, 30 parts distilled water, and 2 parts glacial acetic acid. The material kept in this solution was in excellent condition for sectioning, though, of course, no good fixing of the protoplasmic structure was obtained. That collected from trees *C* and *D* was fixed in Gilson's solution and kept, by mistake, in 95 per cent alcohol. When attempts were made to section it, several months later, considerable difficulty was experienced, because of brittleness. Attempts to soften the material, by allowing it to remain in equal parts of glycerine and alcohol, and also in glycerine alone, proved futile. The greater part of the material was sectioned without imbedding, but some of it was necessarily imbedded in celloidin. The sections were cut from 20 to 40 μ in thickness and stained with safranin and Delafield's haematoxylin of the formula so commonly used for wood staining. The methods employed during the season of 1911 are described subsequently.

INVESTIGATIONS OF 1909

The first cuttings were made on April 19 and at this time the buds located on the 4-, 5-, and 6-year old wood had opened,

the leaves being 1/16 of an inch in length. On the younger wood, the buds were less advanced. This was more marked in the 1- and 2-year old wood. This slower development toward the terminal shoot and apex of the branch held true also for the catkins. The same condition was noted also in several larches which in September produced a new growth of leaves, the result of a drouth, followed by favorable conditions. This earlier development of leaves on the older wood is significant in the light of the subsequent facts concerning the inception of cambial activity.

Cambium in resting condition.—According to Sanio and other investigators the cambium proper consists of a tissue but one cell in thickness, which cells by division produce a row of xylem mother and a row of phloem mother cells. Each of these rows divides and gives rise respectively to two rows of potential xylem cells and two rows of potential phloem cells. Except by careful cytological study the row of true cambium cells cannot be distinguished from the neighboring cells. The term cambium has been, therefore, generally applied to that tissue which lies between the visibly differentiating phloem and xylem. The cambium tissue is composed of a number of rows of cells, which cells are characterized by their thin walls, dense protoplasmic content, and, viewed in cross section, rectangular shape. In trees in the resting condition it would be reasonably assumed that the true cambium comprises the first row of cells just without the xylem. The cells bordering this row on the outside would then be considered as phloem. As a matter of fact, however, sections made from cuttings obtained from the trunk of larch on November 13 exhibit just outside of the xylem a distinct tissue 34 μ in diameter, consisting of five or six rows of cells in thickness. The cells of the outer five rows are not visibly distinguished from cells of the inner row, but are distinguished from the adjacent phloem cells by their size and protoplasmic content. See FIG. 1 and 3. Because of the similarity of all of these cells I have considered the six rows as comprising the cambium tissue, the term cambium being employed in its generally applied sense.

Inception of cambial activity and development of phloem.—The material collected on April 19 showed that cambial activity had begun. The layer of six cambium cells had increased in diameter.

The outer cells of this tissue were losing their rectangular shape and assuming more nearly that of a square, as viewed in a cross section. See FIG. 1, 2, and 3. In studying the slides made from material collected on April 19, it was found that in the 5th, 6th, and 7th cuttings of tree *A* the cambium had developed to a greater extent than in the other cuttings. Not only had the cambium increased in diameter, but seemingly new cells had been formed. This increased development near the middle was maintained until May 25. The average increase in number of phloem cells by May 25 was only 1.8, but the diameter increase of the cambium and phloem was nearly 100 per cent. Up to this time no xylem whatsoever had been developed. It appears therefore that the earliest growth consists in an enlargement of the cambium tissue with the gradual transformation of the peripheral cells into phloem tissue. The old phloem cells adjacent at this time are becoming compressed due to the pressure brought about by the transformation of the cambial cells. Compare FIG. 1, 2, and 3.

In TABLE 1 are given the figures obtained by the measurement of the diameter of phloem and cambium tissues in trees *A* and *C*. The figures for the diameter of the cambium tissue during the resting period (cutting made November 13) are given for comparison. The figures included under the dates April 19 to May 25 inclusive refer to tree *A*. From June 3 to July 6 the figures refer to tree *C*.

As indicated previously, the six-celled layer adjacent to the xylem is considered the cambium. Although transformation of the peripheral cells had occurred, it is difficult to state which cells are cambium and which cells are phloem. Consequently the six rows, despite the transformation, I have considered as cambium. Any cells in excess of the six rows, which lie within the old compressed phloem cells, I have considered as new phloem. After May 25, when xylem and phloem were both developing rapidly, the cambium tissue was still considered as a tissue of six rows of cells. It was difficult to select always the six most uniform rows, but in general the error was slight and at most of little consequence.

From an examination of the table it may be seen that up to May 25 the middle regions show the greatest growth. From April 19 to May 25 the increase in phloem was gradual, but from May 25

TABLE I

NUMBER OF ROWS OF NEW PHLOEM CELLS AND DIAMETER OF PHLOEM AND CAMBIUM TISSUE IN TREES *A* AND *C*

Region of cutting	Nov. 13		Apr. 19		Apr. 26		May 5		May 11		May 25		June 3		June 15		June 30		July 6	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl	0	34	0	34	0	34	0	41	0	58	0	51	7	122	7	146				
Below 2d whorl	0	34	0	54	0	58	1	51	0	58	0	51			9	170				
Below 3d whorl	0	34	0	58	1	68	0	58	0	51	4	75			10	184	12	224		
Below 4th whorl....	0	34	2	58	1	61	0	51	2	68	4	75	10	187	8	184	15	296		
Below 5th whorl....	0	34	1	68	2	71	2	71	3	74	3	85	11	204	9	177	14	278		
Below 6th whorl....	0	34	2	61	1	68	2	74	2	71	3	75	12	221	9	211	14	273		
Below 7th whorl....	0	34	1	68	1	65	1	58	1	68	2	61	11	207	9	191	13	262		
Below 8th whorl....	0	34	0	58	0	48	1	51	1	61	2	58	14	190	14	211	14	278	15	278
Below 9th whorl....	0	34	0	44	0	51	0	51	1	54	0	51	—		11	208		—	16	289
Below 10th whorl...	0	34	0	44	0	51	0	44	0	51	0	51	12	204	10	204		—	12	238
Average.....	0	34	0.6	54.7	0.6	57.5	0.7	55	1.	61.4	1.8	63.3	11	190.7	9.6	189	13.6	268	14.3	268

to June 3 the growth was markedly increased, while from June 3 to June 15 seemingly little growth occurred. After June 3 it appears that relatively few new phloem cells were formed, but growth consisted more of an enlargement of the cells already formed. Some of the figures for June 15 are less than the corresponding figures for June 3. This may be perhaps explained by the fact that the cuttings were made somewhat lower, or better perhaps by the fact that in obtaining these cuttings they were not taken on a line directly below the preceding, but to one side. Mer (loc. cit.) draws special attention to the well-known observation that wood growth is not always uniform on all sides of the tree.

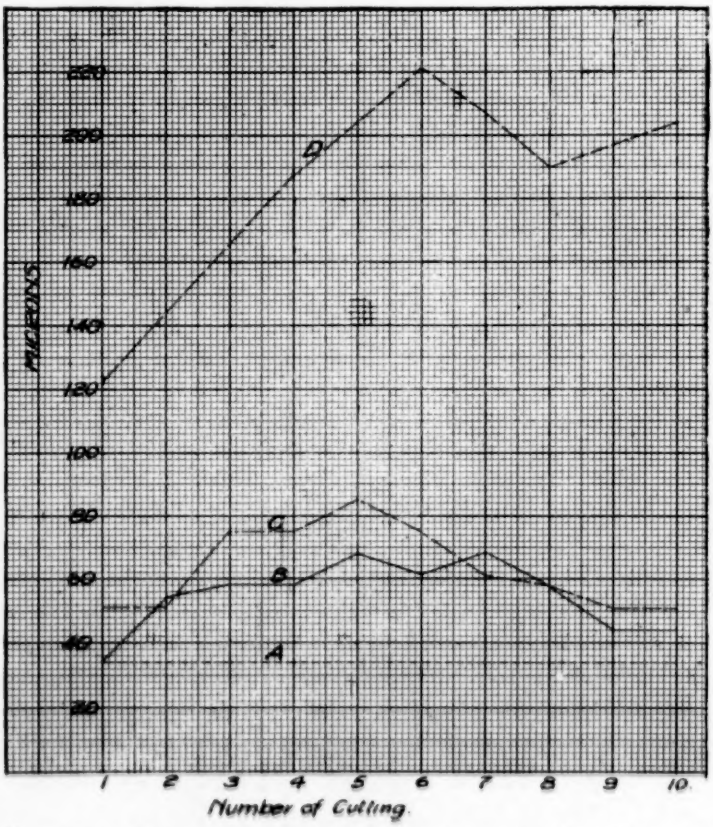

DIAGRAM 1. Diameter of cambium and new phloem at various different dates. *A*, Nov. 13; *B*, April 19; *C*, May 25; *D*, June 3.

By July 6 the phloem was nearly complete with respect to cell numbers; for, the average annual number of rows of phloem cells produced during a period of three years was found to be seventeen. At this time the cells were all very regular in form and no visible differentiation had occurred. In DIAGRAM I are represented the diameter measurements of the phloem at several different dates.

In trees *B* and *D* the growth is similar to that in trees *A* and *C*, though more vigorous growth resulted in tree *B* than in tree *A*. In this tree also the development of cambium consists first in a transformation of the peripheral cells. In this case, however, the number of rows of phloem cells produced by May 25 was 5.6 with nearly a 200 per cent increase in diameter. The detailed figures are given in TABLE II.

TABLE II

NUMBER OF ROWS OF NEW PHLOEM CELLS AND DIAMETER OF PHLOEM AND CAMBIUM TISSUES IN TREES *B* AND *D*

Region of cutting	Nov. 13		May 5		May 11		May 25		June 8		June 18	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl.....	0	34	—		—	75	2	68	8	170	11	228
Below 2d whorl	0	34	0	34	3	58	4	122	11	193	11	218
Below 3d whorl	0	34	3	68	4	82	4	76	—	—	11	286
Below 4th whorl.....	0	34	4	102	4	102	6	92	12	221	14	262
Below 5th whorl.....	0	34	5	85	6	115	—	—	—	—	12	262
Below 6th whorl.....	0	34	4	68	8	107	7	92	10	190	13	238
Below 7th whorl.....	0	34	—	—	4	85	7	102	—	—	14	279
Below 8th whorl.....	0	34	4	85	—	—	6	92	8	170	—	—
Below 9th whorl.....	0	34	2	61	—	—	6	76	8	173	12	245
Below 10th whorl....	0	34	3	75	—	—	6	—	—	—	11	238
Average.....	0	34	3.1	72	4.8	89	5.3	90	9.5	186	12	250

Development of xylem.—While in tree *A* there was a gradual increase in phloem from April 19 to May 25, yet no xylem cells had been formed. During the week of May 25 to June 3, coincident with the marked increase of phloem, a very marked increase of xylem occurred, over one third of the xylem being completed during these seven days. TABLE III gives the figures obtained for the number of rows of xylem cells formed, and the diameter of the xylem tissue in the various cuttings at the different dates. There is included also the diameter of the xylem tissue formed in tree *B* during the years 1909 and 1910. In the first column the

figures refer to tree *A*. The figures from June 3 to July 6 refer to tree *C*.

TABLE III

NUMBER OF ROWS OF NEW XYLEM CELLS FORMED AND DIAMETER OF NEW XYLEM TISSUE IN TREES *A* AND *C*

Region of cutting	May 25	June 3		June 15		June 30		July 6		1909	1910
	No.	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	Dia. μ	Dia. μ
Below 1st whorl . .	0	15	262	25	544	43	1,054			646	986
Below 2d whorl . .	0			33	833	55	1,564			1,598	1,377
Below 3d whorl . .	0	20	578	33	918	48	1,462			1,853	1,870
Below 4th whorl . .	0	29	697	43	1,122	50	1,462			1,785	1,870
Below 5th whorl . .	0	28	748	45	1,292	55	1,530			1,360	1,955
Below 6th whorl . .	0	23	646	46	1,326	58	1,666			1,275	1,224
Below 7th whorl . .	0	24	648	36	1,122	57	1,515			1,734	1,428
Below 8th whorl . .	0	22	714	36	1,156	57	1,632	65	1,972	2,363	1,598
Below 9th whorl . .	0	—	697	28	850		—	62	1,870	1,666	1,088
Below 10th whorl.	0	20	663	27	833	58	1,564	58	1,802	—	—
Average.	0	22.5	628	35.2	999.6	53.3	1,493	61.6	1,881	1,586	1,488

From the table it cannot be determined exactly in which part of the tree xylem growth first begins. The greatest growth by June 3 was below the fifth whorl of branches while the least growth was just below the first whorl of branches. In general, by June 3 more xylem cells were formed in the middle of the tree than at either the top or base. This would tend to indicate that the first growth of xylem occurred in the middle of the tree below the fifth whorl of branches.

TABLE IV

NUMBER OF ROWS OF NEW XYLEM CELLS AND DIAMETER OF NEW XYLEM TISSUE IN TREES *B* AND *D*

Region of cutting	May 11	May 25		June 8		June 18	
	No.	No	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl.	0	0	0	22	442	43	1,003
Below 2d whorl.	0	0	0	40	647	53	1,326
Below 3d whorl.	0	0	0	—	—	55	1,394
Below 4th whorl.	0	4	51	35	918	50	1,258
Below 5th whorl.	0	—	—	—	—	45	1,292
Below 6th whorl.	0	5	55	32	850	46	1,122
Below 7th whorl.	0	2	20	—	—	55	1,258
Below 8th whorl.	0	0	0	34	850	—	—
Below 9th whorl.	0	0	0	30	782	50	1,292
Below 10th whorl.	0	0	0	—	—	49	1,292
Average.	0	1.2	14	32	748	49	1,238

TABLE V

TOTAL NUMBER OF ROWS AND DIAMETER INCREASE OF PHLOEM, CAMBIUM, AND XYLEM CELLS IN TREES *A* AND *C*

Region of cutting	Nov. 13		Apr. 19		Apr. 26		May 5		May 11		May 25		June 3		June 15		June 30		July 6	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl....	6	34	5	34	5	34	7	41	7	58	6	51	28	384	38	690	—	—		
Below 2d whorl	6	34	6	51	7	54	6	51	6	58	6	51	—	—	48	1,003	—	—		
Below 3d whorl	6	34	6	51	6	58	6	58	6	51	10	75	—	—	49	1,101	66	1,686		
Below 4th whorl....	6	34	8	68	6	62	8	51	8	68	10	75	45	884	58	1,305	71	1,758		
Below 5th whorl....	6	34	7	61	8	71	9	71	9	68	9	85	45	952	60	1,468	75	1,741		
Below 6th whorl....	6	34	7	75	8	68	8	75	8	71	9	75	41	867	62	1,536	78	1,945		
Below 7th whorl....	6	34	7	58	7	65	7	58	7	68	7	61	41	853	53	1,312	76	1,842		
Below 8th whorl....	6	34	6	51	7	48	7	51	7	61	7	58	42	935	56	1,332	77	1,910	86	2,251
Below 9th whorl....	6	34	6	44	6	51	7	51	7	54	6	51	—	—	45	1,057	—	—	84	2,125
Below 10th whorl...	6	34	6	44	6	51	6	51	6	51	6	51	38	867	43	1,037	—	—	76	2,040
Average.....	6	34	6.4	53.7	6.6	56	7.1	55.8	7.1	60.8	7.5	63.3	40	820	51.2	1,184	73.8	1,813	82	2,138

While in trees *A* and *C* the region of the first growth of xylem could not be definitely located, more fortunate results were obtained with tree *B*. No xylem was formed in tree *B* until May 25 and then neither at the top nor at the base of the trunk, but in the middle region. By May 25 then the xylem in that part of the tree between the fourth and fifth whorls of branches was four cells in thickness,—while between the sixth and seventh whorls it was five cells and between the seventh and eighth it was two cells in diameter. The most marked development again occurred immediately after May 25. The detailed figures are given in TABLE IV.

Season and duration of diameter increase.—In order to bring out more clearly the period of greatest diameter increase, the combined values for increase of phloem, cambium, and xylem, in trees *A* and *C* are given in TABLE V.

From the table it is at once evident that very little growth took place previous to May 25, and the growth which occurred was confined, as before indicated, entirely to the cambium and phloem. From May 25 to June 3 a very marked increase occurred, and during that time in the middle regions of the trunk nearly one half of the total diameter increase was completed. In TABLE VI is given the daily average increase in rows of cells and also the daily diameter increase in trees *A* and *C*.

TABLE VI

Period	May 25–June 3	June 3–June 15	June 15–June 30	June 30–July 6*
No. rows of cells	4.2	1.	1.4	1.
Dia. in microns	94.5	30.	40.	48.

By July 6 the ring of xylem was almost complete, judging from the extent of the summer wood which was then in the process of formation, though not yet completely developed. Unfortunately no further series of cuttings were made after July 6 to determine the succession with regard to growth cessation.

In TABLE VII is given the combined diameters of the phloem, cambium, and xylem tissue in trees *B* and *D*, as well as the total number of cells.

* For cutting nos. 9–10 only.

TABLE VII

TOTAL NUMBER OF NEW ROWS AND DIAMETER OF PHLOEM, CAMBIUM AND XYLEM CELLS IN TREES *B* AND *D*

Region of cutting	Nov. 13		May 5		May 11		May 25		June 8		June 18	
	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ	No.	Dia. μ
Below 1st whorl....	6	34	—	—	10	75	8	68	36	612	60	1,231
Below 2d whorl....	6	34	6	34	9	58	11	89	57	840	70	1,544
Below 3d whorl....	6	34	9	68	10	88	10	75	—	—	72	1,680
Below 4th whorl...	6	34	10	102	10	102	16	143	53	1,071	70	1,520
Below 5th whorl....	6	34	11	85	14	115	—	—	—	—	63	1,486
Below 6th whorl....	6	34	10	68	15	108	18	147	48	1,040	65	1,506
Below 7th whorl....	6	34	—	—	11	85	14	122	—	—	77	1,537
Below 8th whorl....	6	34	10	85	—	—	12	92	48	986	—	—
Below 9th whorl....	6	34	8	61	—	—	12	76	44	955	68	1,537
Below 10th whorl...	6	34	9	75	—	—	—	—	—	—	62	1,530
Average.....	6	34	9	72	11	90	12.6	101.5	47.5	917	69.4	1,508

The season of diameter growth in larch is relatively short. Practically all of the growth occurred during the month of June. The small increase produced from the time of bud opening, April 19 to May 25, consisted entirely of cambium and phloem development. The diameter increases of trees *A* and *C* and *B* and *D* during the season 1909 are graphically represented in DIAGRAM II.

INVESTIGATION OF 1911

Since the studies made in 1909 indicated that growth in diameter first occurred in the middle region of the trunk and not at the base or apex, it seemed advisable to continue these studies with respect to the development in the lateral branches. The investigation was made with the object of answering the three following questions: (1) Does inception of diameter increase begin first in the topmost branches, in the middle, or in the basal, branches? (2) In what part of the individual branches does diameter increase begin? (3) Does xylem development in the lateral branches precede that in the trunk?

For this investigation a larch tree of approximately 10 years of age was used. It was growing isolated, about 100 feet from the trees mentioned above, growing in the nursery row. For convenience this tree is hereafter designated as tree *E*. On May 22, from each of the whorls of branches from apex to base, one branch

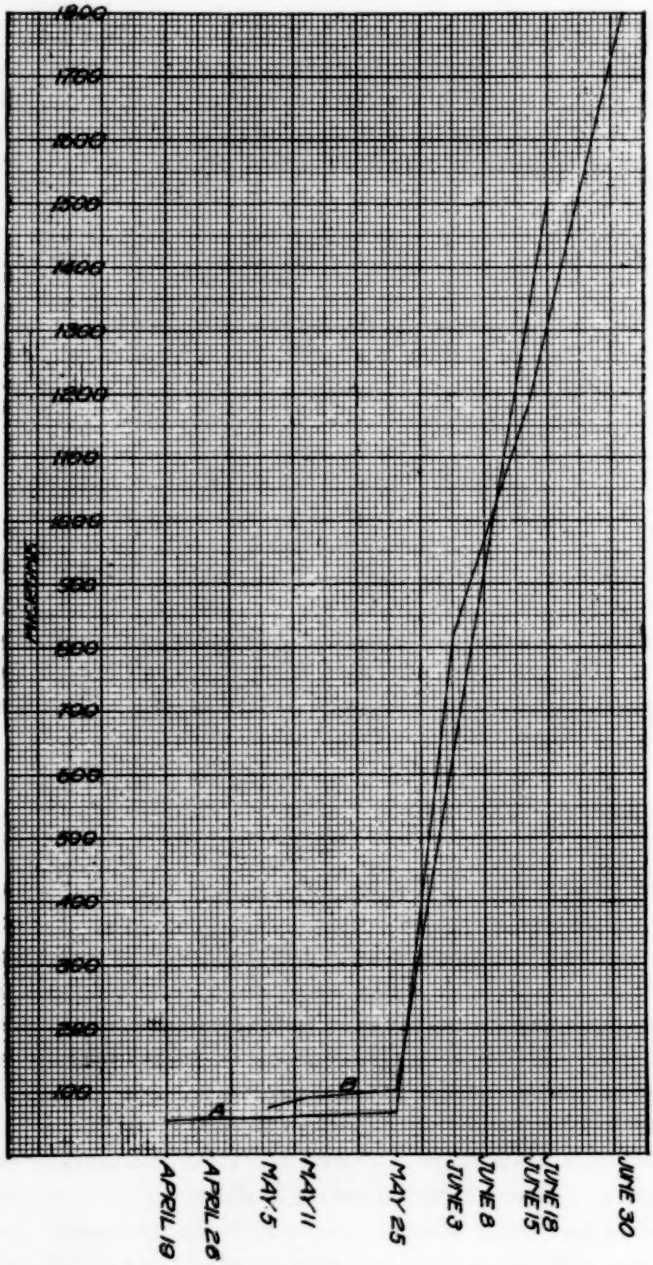

DIAGRAM II. *A*, diameter increase in trees *A* and *C*; *B*, diameter increase in trees *C* and *D*.

was removed. The removal, as before, was made from the south side of the tree. The branches were numbered according to their position on the tree, the topmost branch being No. 1, and the basal branch No. 7. From the individual branches there was removed from each season's growth a cutting; from the topmost branch two such cuttings were removed and from the basal branch

TABLE VIII

NUMBER OF ROWS OF XYLEM CELLS AND DIAMETER INCREASE OF XYLEM TISSUE IN THE CUTTING FROM LATERAL BRANCHES OF TREE *E*

No. of branch	Region of cutting on lateral branch	No. of rows of new xylem cells	Diameter increase of xylem
1	Below 1st whorl	0	0
1	Below 2d whorl	0	0
2	Below 1st whorl	0	0
2	Below 2d whorl	0	0
2	Below 3d whorl	0	0
3	Below 1st whorl	2	37 μ
3	Below 2d whorl	2	37 μ
3	Below 3d whorl	0	0
3	Below 4th whorl	0	0
4	Below 1st whorl	2	37 μ
4	Below 2d whorl	1	18 μ
4	Below 3d whorl	2	37 μ
4	Below 4th whorl	0	0
5	Below 1st whorl	2	29.6 μ
5	Below 2d whorl	1	18 μ
5	Below 3d whorl	0	0
5	Below 4th whorl	2	37 μ
5	Below 5th whorl	0	0
5	Below 6th whorl	0	0
6	Below 1st whorl	2	37 μ
6	Below 2d whorl	0	0
6	Below 3d whorl	0	0
6	Below 4th whorl	1	18 μ
6	Below 5th whorl	2	37 μ
6	Below 6th whorl	0	0
6	Below 7th whorl	2	18 μ
7	Below 1st whorl	0	0
7	Below 2d whorl	0	0
7	Below 3d whorl	1	18 μ
7	Below 4th whorl	0	0
7	Below 5th whorl	1	18 μ
7	Below 6th whorl	0	0
7	Below 7th whorl	0	0
7	Below 8th whorl	0	0

seven cuttings. These cuttings were fixed, sectioned, and prepared as before. In the following table the figures given refer only to the number of cells in the new xylem layer and to the diameter of that tissue. The diameter increase over the entire tree is represented in DIAGRAM III.

In order to show more clearly the results obtained and to aid in the interpretation the following two tables have been compiled from the preceding. In the TABLE IX are presented for each of the branches the average number of rows of xylem cells and the average diameter increase of the xylem tissue for the entire lateral branch. The averages are obtained from the figures for each individual cutting.

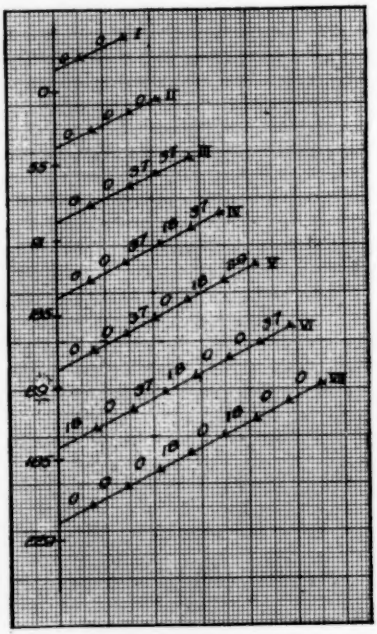

DIAGRAM III. Diameter increase of xylem in various parts of tree *E* on May 2

TABLE IX

AVERAGE DIAMETER INCREASE OF XYLEM IN LATERAL BRANCHES

Branch	Average no. of rows of new xylem cells	Average diameter increase of xylem
I	0	0 μ
II	0	0 μ
III	1	18 μ
IV	1.25	23 μ
V	0.83	14.1 μ
VI	1	15.7 μ
VII	0.25	4.5 μ

From the above table it is evident that the least growth occurred in the top and basal branches and the greatest growth

in the middle branches. This increase corresponds with the results secured previously on the diameter increase in the trunk, in which it was found that the growth first began in the middle region.

In regard to the second question as to the region of the branch in which growth first occurs, TABLE X is suggestive. The figures of the following table are the averages of the seven apical cuttings, the seven basal cuttings and the average diameter of xylem in the middle regions of the seven branches.

TABLE X

AVERAGE DIAMETER INCREASE OF XYLEM AT APEX, MIDDLE, AND BASE OF ALL LATERAL BRANCHES

Region of cutting	Diameter increase of xylem
Apical	20.8μ
Middle	7.5μ
Basal	2.5μ

From previous results it was expected that the growth would first occur in the middle of the branch, but the evidence indicates that the development of xylem in the lateral branches begins at the apex and then continues towards the base. The opening of the buds, however, does not follow the same order. On April 26, 1911, the lateral branches of a tree in the nursery row were examined and it was found that buds on the one and two years old wood had not yet opened, on the third year wood the leaves were just protruding while on the older wood the buds were fully opened.

In regard to the third question, "Does diameter increase in the twigs and branches precede that in the trunk?" the following observations were made. From the same tree from which the cuttings from the lateral branches were removed and on the same day,—namely, May 22, cuttings were removed from the apex to the base of the trunk. Seven such cuttings were removed from the south side of the tree, one cutting just below each whorl of branches. From a study of slides prepared from the material the following figures have been obtained. (See TABLE XI.) There are also included in TABLE XI figures derived from cuttings made on June 6.

A comparison of the figures for May 22 with the figures for growth in the lateral branches (see DIAGRAM III) reveals the fact

TABLE XI

NUMBER OF ROWS OF XYLEM CELLS AND DIAMETER INCREASE OF XYLEM IN TREE *E*

Region of cutting	No. May 22	Diameter increase of xylem May 22	No. June 6	Diameter increase of xylem June 6
Below 1st whorl . . .	0	0	——	——
Below 2d whorl . . .	3	55.5 μ	5	111 μ
Below 3d whorl . . .	5	91 μ	7	139.5 μ
Below 4th whorl. . .	7	185 μ	——	——
Below 5th whorl. . .	4	88.8 μ	9	259 μ
Below 6th whorl. . .	7	185 μ	17	444 μ
Below 7th whorl. . .	9	229.4 μ	20	481 μ
Average.	5.8	139 μ	9.8	286 μ

that except for the apical part of the trunk the growth there has been much greater than in the branches. The average diameter increase of xylem in all the branches was by May 22 only 10.7 μ, and the average number of cells in the new xylem layer only 0.62. The greatest diameter increase in the branches was only 37 μ, while the average for the trunk was 5.8 cells with a diameter of 139 μ. If reference is made to TABLE VIII it will be seen that no growth occurred in branch No. 2 while in the trunk at this region the increase was 55.5 μ. The average diameter of xylem in branch No. 7 was only 4–5 μ, while in the region of the trunk from which the branch was secured the diameter increase amounted to 229 μ. It is very evident, therefore, that in a larch of this age under isolated conditions growth does not begin first in the twigs and then extend to the trunk, but rather it begins first in the trunk.

The figures in TABLE XI give no strong indication of the region in which growth first began. The diameter increase was greatest just below the 4th, 6th, and 7th whorls of branches. No increase was manifest near the apex.

TABLE XII

Region of cutting in trunk	No. of rows of xylem cells	Dia. increase of xylem
Below 1st whorl.	Cutting lost	——
Below 5th whorl.	4	111 μ
Below 7th whorl.	9	222 μ
Below 9th whorl.	5	129 μ

In order further to check the work of 1909 a few cuttings were made from another tree in the nursery row on May 22. This tree

was now approximately 15 years of age. Cuttings were removed from the south side of the trunk below the 1st, 5th, 7th, and 9th whorls of branches. The results from the measurement of the xylem are found in TABLE XII.

While no conclusions can be drawn respecting the inception of growth the indications again point to the middle region. The figures are of interest mainly because of the fact that growth of xylem has occurred before May 25, which was the date of xylem development in 1909.

FACTORS INFLUENCING DATE OF XYLEM FORMATION

Temperature, moisture, and insolation are important factors in all growth phenomena. In 1909 and 1911 the opening of buds of larch began April 19. In 1909 the xylem formation began on May 25, while in 1911 the xylem formation began about May 20.* The temperature, moisture, and sunshine figures for the intervals between the bud opening and wood formation are found in the following table. The mean temperature for the day is considered as the number of heat units for that day, and the total heat units† is considered as the sum of these mean temperatures.

Period	Total heat units	Hours of sunshine	Precipitation
April 19—May 25, 1909...	1,810	234.5	2.89
April 19—May 20, 1911...	1,769	257.	2.00

The number of heat units then during the interval before wood formation in 1911 was almost as great as that during the longer period of 1909, while the amount of sunshine was greater during the 1911 period. The amount of precipitation at this time of the year was not important as sufficient water was available both seasons. In 1911, however, the mean temperature for the three days preceding wood formation ranged from 76° F.–78° F. and for the three days preceding this period the range of the mean temperatures was 62° F.–69° F. During 1909 the nine days preceding wood formation ranged in mean temperature from 50° F.–54° F. except one day which had a mean temperature of 58. The three

* The exact date of xylem formation was not determined. The observation on May 22 showed a diameter increase of 6 cells.

† No daily mean temperature was below 34° F.

days preceding wood formation in 1909 had 39.4 hours of sunshine; the same period in 1911 had 26.2 hours of sunshine. It is very probable therefore that during 1911 the relatively higher temperature for the six days preceding wood formation was important in hastening the inception of xylem formation.

SUMMARY

RESULTS OF 1909. (1) *Cambium and phloem development.*—The cambium in the trunk during the resting condition consists of six rows of cells 34 μ diameter. On April 19 the first material collected exhibited an increase in diameter of the cambium tissue. The cambium cells were all enlarged while the outer cells were in the process of transformation, changing from a rectangular to square shape as viewed in cross section. In the middle regions of the trunk on April 19 an increase in phloem cells was evident. The increase of cambium and phloem was gradual over the entire trunk in tree *A* up to May 25, the greatest increase being maintained in the middle region. Similar conditions were found in tree *B*, though here the increase of new phloem cells was more marked. The greatest growth of phloem occurred immediately after May 25 and was coincident with the greatest development of xylem.

(2) *Xylem development.*—In tree *A* no xylem was formed before May 25. In tree *B* a few xylem cells were formed by May 25 in the middle regions of the trunk. Growth of xylem was almost simultaneous, however, in all parts of the trunk. The greatest growth occurred immediately after May 25 and in tree *C* the xylem was nearing completion by July 6.

RESULTS OF 1911.—(1) Growth in diameter in the lateral branches begins first in the middle branches and is followed by that in the basal and apical branches.

(2) In the individual branches growth begins first at the apex and then descends towards the base.

(3) Diameter increase of the trunk precedes that in the branches and twigs.

(4) Temperature and insolation conditions in 1911 induced wood formation five days earlier than in 1909.

(5) No direct evidence was secured in 1911 concerning the

region in the trunk of first cambial activity. Indications pointed again to the middle and basal regions.

DISCUSSION OF RESULTS

In a number of anatomical text books it is stated that the xylem development precedes that of the phloem. This idea is conveyed rather ambiguously by Stevens.* In the American larch the development of phloem certainly precedes that of xylem and its most rapid development is coincident with that of the xylem. Brown's† figures indicate that in *Pinus rigida* a similar condition prevails.

The results obtained by the writer do not agree with those of Th. Hartig‡ with 30-year old European larch, wherein diameter increase near the base of the trunk was two to four weeks later than that in the twigs and branches. The factors which may operate to cause this difference are considered subsequently. My results agree with those of Brown§ who finds that in *Pinus rigida* the first diameter increase of xylem begins a few meters below the apex. The work of Brown was done during the same period as that of the writer and on trees in a plot adjacent to those used in this investigation.

Respecting the date of diameter increase Buckhout states that in European larch it is coincident with leaf formation. It is very probable that the diameter increase at this time is due mainly to a swelling of the tissues. In my investigations the development of xylem began a month later than the beginning of leaf formation. From observations made during the past two years with a considerable number of trees and from the results of other investigators it seems probable that in general growth in diameter does not begin until the leaves have been fully developed and have been sufficiently active in food making to supply the requirements of rapid cell formation. The reserve foods stored up in the fall are probably largely utilized in leaf and also in blossom formation, when the latter precede the formation of leaves.

* Stevens, W. C. Plant anatomy, 2nd Ed., p. 170. 1910.

† Brown, H. P. Growth studies in forest trees, I. *Pinus rigida* Mill. Bot. Gaz. **54**: 386–402. 1912.

‡ Hartig, T., loc. cit.

§ Brown, H. P., loc. cit.

What factors operate to cause growth inception in a particular part of a tree? Robt. Hartig* believed that temperature was the most important factor, consequently insolation, temperature of the air and of the soil moisture, and thickness of the bark are the essential factors which determine the region of first diameter increase. No doubt these factors are important, as considerable evidence indicates that in old trees diameter increase is delayed at the base of trunk where insolation is poor and the bark is thick. In young trees, however, these are not the only factors. In the larch trees of 13 years of age the diameter increase did not begin first in those regions with the thinnest bark and best insolation. The thickness of the bark at the apex, middle and base of the tree *A* was respectively 596 μ, 1,937 μ, and 3,278 μ. So also in the isolated tree *E* the inception of diameter increase did not occur in the parts of the tree best insolated and with the thinnest bark, but rather in the thicker barked and more poorly insolated parts of the tree, namely the middle and basal regions of the trunk. In the individual branches, however, growth in diameter began in the regions of thinnest bark and of best insolation.

Whitten† has shown that the color of the bark may be important in the time of growth inception of buds. The color of the bark may be a factor in determining the region of diameter increase in young trees of larch. The color of the bark of the apical part of the trunk in spring is yellowish to greenish, becoming darker towards the base. The darker color, because of its capacity for heat absorption, may counteract the insulating effect of the thick bark, consequently the diameter increase begins in the basal and middle regions. The growth begins first in the middle regions because the bark here is of the same color as that of the basal regions and is only about half as thick. The fact that in the branches and twigs of larch the opening of buds on the apical regions is retarded is suggestive of the influence of the color of the bark. The bark of the apical regions being of lighter color less heat is absorbed, its temperature therefore is lower and the development of the buds is slower. This is in agreement with the

* Hartig, R., loc. cit.

† Whitten, J. C. Winter protection of the peach. Missouri Agr. Exp. Sta. Bull. 38: 140–164. 1897.

results obtained by Whitten* on the date of blossoming of green- and purple-twigged peach trees.

The temperature of the soil moisture and of the air, and the thickness and color of the bark are not the only factors operative in inducing diameter increase. Certainly as regards all of the above factors the branches are all more favored than the trunk of the tree, yet in the isolated tree *E* the diameter increase began first in the trunk. Food supply may be a factor in stimulating the cambium of the trunk to diameter increase, before there is development in the branches. It is not possible to state the influence of food supply. Controlled experimental work with this as well as with the other factors is necessary to give an idea of the influence of each in stimulating the cambium to activity.

In conclusion it should be stated that considerably more work is necessary in order to establish the region of the tree in which cambium activity first begins. No doubt different conditions will be found for trees of the same species of different ages, and for trees of different species and genera. Investigations of this character are important because only by such studies can the factors be determined which stimulate cambium activity. It is essential also to determine the period and extent of phloem and xylem formation in trees and the duration of cambium activity. Much more work remains to be done along this line. Such work is of especial importance in fruit culture and in a subsequent paper the results of such an investigation will be presented.

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Explanation of figures

FIG. 1. Cutting no. 6 made from trunk on November 13, showing cambium tissue *a* to *a*, consisting of six rows of cells; ×475.

FIG. 2. Shows extent of cambium in basal cutting, No. 10, made on May 5. Compare with Fig. 2; ×475.

FIG. 3. Cutting no. 6 taken from trunk of tree *A* on May 5. Cambium *a* to *a*. Note the increased diameter and cell differentiation; ×475.

FIG. 4. Cutting no. 5 made on May 25 from tree *A*. Xylem formation not yet begun; ×33.

FIG. 5. Cutting no. 4 from tree *C* made on June 3; ×33.

FIG. 6. Cutting no. 7 from tree *C* made on June 30; ×33.

FIG. 7. Cutting no. 8 from tree *C* made on July 8. Differentiation of summer wood is beginning; ×33.

* Whitten, J. C., loc. cit.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1910–1913)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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